The Auk 110(3):445-457, 1993

TEMPERATURE REGULATION IN NEONATES OF SHOREBIRDS

G. HENK VISSER[1,3] AND ROBERT E. RICKLEFS[2]
[1]*University of Utrecht, Department of Veterinary Basic Sciences Division Physiology, P.O. Box 80.176, 3508 TD Utrecht, The Netherlands; and*
[2]*Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104, USA*

ABSTRACT.—In the laboratory we determined cooling rates, resting and peak metabolic rates, and minimal thermal conductances in neonates of nine North American and five European shorebird species, with neonatal body masses between 4 and 55 g. We measured the initial (T_i) and final body temperature (T_f) of chicks during 30-min exposures to an ambient temperature (T_a) of 18°C. For each trial, the change in body temperature was converted to an index of homeothermy (H) by dividing the final temperature difference between the chick and surrounding air by the initial difference, such that $H = (T_f - T_a)/(T_i - T_a)$. The interspecific relation between H and body mass (M; grams) could be described by $H = 0.073 + 0.464 \log_{10}(M)$. Among neonates, the interspecific relationships of effective net peak metabolic rate (peak metabolic rate minus the evaporative heat loss) to body mass could be described by PMR_n ($W \cdot ind^{-1}$) $= 0.0161M^{0.922}$, of minimal dry thermal conductance (minimal thermal conductance minus the evaporative heat loss) by h_{na} ($W \cdot {}^{\circ}C^{-1} \cdot ind^{-1}$) $= 0.0114M^{0.359}$, and of the ratio between heat production and heat loss by $PMR_n/h_{na} = 1.412M^{0.563}$. Thus, the higher degree of homeothermy in larger neonates could be explained by their more favorable ratio of heat production to heat loss. Peak metabolic rates of shorebird neonates were 1.9 times the resting metabolic rates in the zone of thermoneutrality. Rate of decrease in body temperature could be adequately simulated with a Newtonian cooling model that incorporated metabolic measurements corrected for evaporative heat loss. The degree of homeothermy of shorebird neonates appears to be related primarily to body mass. The occupation of cold, arctic regions during the breeding season by some species does not depend on adjustment of either minimal thermal conductance or thermogenic heat production by neonates, compared to other species that breed in more temperate climates. *Received 31 October 1991, accepted 1 September 1992.*

WITHIN THE families Charadriidae and Scolopacidae (often referred to as shorebirds or waders), neonatal body mass varies between 4 and 55 g (Johnsgard 1981). According to the classification of Nice (1962), neonates of almost all shorebirds are precocial: they hatch open-eyed, downy, and mobile. The chicks are self-feeding, and only guided and brooded by their parents. However, Nice's classification does not allow for the possibility that body size influences the degree of precocity of the growing chick. The greater thermal inertia of larger chicks may make it possible for them to regulate their body temperature at a younger age. The purpose of our study was to explore the influence of body mass on the thermal independence of shorebird neonates.

Many shorebird species (especially those in the Scolopacidae) inhabit temperate and arctic grasslands and tundra. Chicks of these species allocate their time between alternating bouts of foraging and parental brooding (Beintema and Visser 1989a, Visser 1991). The time available for foraging depends upon the chick's degree of homeothermy and the ambient temperature. At low ambient temperatures, especially, small chicks cool rapidly, restricting them to foraging during less than 30% of the daytime. During adverse weather, some chicks die of starvation. Thus, degree of homeothermy and survival are closely linked through the chick's time budget. Owing to a more favorable surface-to-volume ratio for retaining body heat, larger chicks should be less sensitive to the adverse effects of cold temperature on foraging time. This factor thus might be expected to exert strong selection for large body size of the neonatal shorebird chick.

In this study we investigated the relationship between neonatal body mass and degree of homeothermy in shorebirds. We determined the

---

[3] Present address: Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands, and Centre for Isotope Research, University of Groningen, Nijenborgh 4, 9747 AG Groningen, The Netherlands.

TABLE 1. List of abbreviations and units.

C	Heat capacitance of the animal (J·°C^{-1})
E	Evaporative heat loss (W)
H	Index of homeothermy (dimensionless)
h	Minimal thermal conductance (mW·°C^{-1}·g^{-1})
h'	Thermal conductance (mW·°C^{-1}·g^{-1})
h_n	Dry thermal conductance (mW·°C^{-1}·g^{-1})
h_{na}	Dry thermal conductance per animal (W·°C^{-1})
LCT	Lower critical temperature (°C)
M	Body mass (g)
PMR	Peak metabolic rate of heat production (W)
PMR_n	Effective net peak metabolic rate of heat production (W)
RMR	Resting metabolic rate in the thermoneutral zone (W)
t	Time (s)
T_a	Ambient temperature (°C)
T_b	Body temperature (°C)
T_e	Equilibrium body temperature (°C)
T_f	Final body temperature (°C)
T_i	Initial body temperature (°C)
W	Metabolic heat production (W)

change of body temperature during cooling trials at an ambient temperature of 18°C in neonates of nine North American and five European shorebird species covering the mass range between 4 and 55 g. We also measured neonatal resting and peak metabolic rates, in addition to minimal thermal conductances, of these species. We compared our results for shorebirds with literature data for neonates of other families having precocial and semiprecocial modes of development.

MATERIALS AND METHODS

Incubation of eggs.—We studied neonates of the Ruff (*Philomachus pugnax*), Common Redshank (*Tringa totanus*), Northern Lapwing (*Vanellus vanellus*), Black-tailed Godwit (*Limosa limosa*) and Eurasian Curlew (*Numenius arquata*)—which we refer to as the European species—at Utrecht, The Netherlands (52°06'N, 5°07'E). The Red-necked Phalarope (*Phalaropus lobatus*), Least Sandpiper (*Calidris minutilla*), Dunlin (*Calidris alpina*), Semipalmated Plover (*Charadrius semipalmatus*), Stilt Sandpiper (*Micropalama himantopus*), Lesser Yellowlegs (*Tringa flavipes*), Lesser Golden-Plover (*Pluvialis dominica*), Hudsonian Godwit (*Limosa haemastica*) and Whimbrel (*Numenius phaeopus*)—which we refer to as North American species—were studied at Churchill, Canada (58°45'N, 93°00'W). European species were studied during the summers of 1986–1988, and the North American species in the summer of 1979. Eggs were collected in the vicinity of Utrecht and Churchill and placed in an incubator (Pas Reform Combi 41 in Utrecht, and Hovabator in Churchill) at 37–38°C and a relative humidity of about 60%.

Rate of body cooling.—After hatching, the chicks were allowed to dry and to fully expand their plumage. In all experiments, the chicks were between 6 and 20 h of age.

To determine the degree of homeothermy, we placed neonates separately for 30 min in a chamber where the temperature was kept constant at 18°C. This temperature was chosen because the body temperature of large neonates dropped a small amount and that of small neonates dropped, but not so much that it precluded taking a 30-min measurement. Before and after each trial, we measured body temperature by inserting a calibrated thermistor probe (Yellow Springs Instruments or Therm 2236-1 with an accuracy of 0.1°C) to a depth of 1 to 2 cm into the rectum (Utrecht) or the proventriculus (Churchill). After each trial we weighed the chick on either Mettler PT-1200 or triple-beam balances to the nearest 0.1 g. For each trial the index of homeothermy (H) was calculated by dividing the final temperature difference between the chick and surrounding air by the initial difference:

$$H = (T_f - T_a)/(T_i - T_a), \quad (1)$$

where T_f and T_i are final and initial body temperatures, respectively, and T_a is the ambient temperature. The index is equal to 1 when body temperature is maintained without change, and 0 when body temperature falls to the ambient level within 30 min. For further details, see Ricklefs (1987). A list of abbreviations is given in Table 1.

Metabolic rates.—We measured metabolism of neonates of the Ruff (n = 14), Common Redshank (n = 23), Northern Lapwing (n = 30), Black-tailed Godwit (n = 31) and Eurasian Curlew (n = 29) at ambient temperatures between 15 and 40°C. The same chick was never used in more than three trials. Single chicks were placed (during the daylight period) in an open flow circuit consisting of an airtight metabolic chamber, which was placed in a darkened climatic chamber. Flow rates (measured with a wet precision gasmeter) were adjusted to maintain the oxygen concentration of the outlet air above 20%. Oxygen and carbon-dioxide levels were measured continuously with a Taylor Servomex OA184 and a Leybold-Heraeus Binos infrared CO_2 analyzer, respectively, with a full-scale deflection of 1%. After an equilibration period of 30 min, readings were continued until the level of gas exchange remained at a constant value over 15 min. This 15-min average was defined as the metabolic rate. After the trial the chick's body temperature was measured and the chick was weighed (see above). The metabolic heat production (*W*; Watts) of the neonate was calculated by the equation

$$W = 4.49\dot{V}O_2 + 1.39\dot{V}CO_2, \tag{2}$$

where $\dot{V}O_2$ and $\dot{V}CO_2$ are the volumes of the oxygen consumed and carbon dioxide produced, respectively, expressed in $1(\text{STPD})\cdot h^{-1}$ (modified from Romijn and Lokhorst 1961).

For the other species, studied at Churchill, metabolic rates of neonates were measured in a closed respirometer containing soda lime to absorb carbon dioxide and drierite to absorb water vapor. The chamber was fitted with a manometer, and oxygen was injected with a calibrated syringe to maintain a constant pressure within the system. Trials included a 20-min equilibration period and a 30-min measurement period. Volume of oxygen added to the chamber was converted to standard temperature and pressure. Values for oxygen consumption were converted to heat production by taking an energy equivalent of $20.0\ kJ\cdot lO_2^{-1}$ (Ricklefs and Roby 1983).

For each European species, the resting metabolic rate in the zone of thermoneutrality (*RMR*) was determined by fitting the metabolic data against ambient temperature with the Scholander model (Scholander et al. 1950). First, an arbitrary value for the lower critical temperature (*LCT*) was assigned by visual inspection of the data. Below this temperature, heat production was assumed to be a linear function of ambient temperature; above the *LCT*, the heat production was assumed to be a constant. Next, the value of the *LCT* was varied in steps of 0.1°C until the best fit was found (lowest residual sum of squares). In the neonates of the Ruff, Common Redshank, Northern Lapwing, Black-tailed Godwit, and Eurasian Curlew the best fit was obtained for lower critical temperatures of 34.6, 34.6, 34.9, 34.6, and 31.2°C, respectively. The other species were considered to be in the thermoneutral zone at ambient temperatures close to 35°C.

The peak metabolic rate of heat production (*PMR*) was determined during 30-min sessions at ambient temperatures below the zone of homeothermy (15–25°C) when chicks were cooling at a maximum of 5°C in 30 min, ensuring that the metabolic rate initially was at maximum. Before and after each trial the body temperature was taken. Metabolic rates were calculated as moving averages of 10-min intervals, with peak metabolic rate being the maximum observed.

For each metabolic measurement the thermal conductance (h', $mW\cdot °C^{-1}\cdot g^{-1}$) was calculated by

$$h' = (W + A)/((T_b - T_a)M), \tag{3}$$

where W is the metabolic heat production (mW), A is a correction factor for the fall in body temperature (mW) during the session, based on a specific heat of $3.45\ J\cdot g^{-1}\cdot °C^{-1}$ (Hart 1951), T_b and T_a are the average body and ambient temperatures, respectively (°C), and M stands for body mass (g). The minimum thermal conductances (h) for the European species were determined following McNab (1980). They were always minimal at ambient temperatures below 30°C. For the North American species, thermal conductances were assumed to be minimal below 30°C.

Newtonian cooling model.—The data on peak metabolic rate and minimal thermal conductance, as derived from metabolic measurements, were used to simulate body temperatures by using a Newtonian model of body cooling. The data on peak metabolic rate (*PMR*) and minimal thermal conductance (h) have to be corrected for the evaporative heat loss (Bakken 1976), resulting in the effective net peak metabolic rate (PMR_n) and minimal dry thermal conductance (h_n). The heat loss due to evaporation (E; W) below the thermoneutral zone for different body masses (M; g) was estimated with an equation derived from data on neonates of four shorebird species, covering the mass range between 14 and 55 g,

$$E = 0.00471M^{0.715} \tag{4}$$

(Visser 1991). The latent heat of vaporization of water was taken as $2.427\ kJ\cdot g^{-1}$ water vaporized (Schmidt-Nielsen 1975). We used the following equation to simulate cooling curves of the neonates (Van Beek pers. comm.):

$$\begin{aligned} T_b - T_a &= (T_i - T_a)e^{-th_{na}/C} \\ &\quad + (PMR_n/h_{na})(1 - e^{-th_{na}/C}), \end{aligned} \tag{5}$$

where T_i stands for initial body temperature (°C), T_b for body temperature (°C), T_a for ambient temperature (°C), h_{na} for minimal dry thermal conductance per individual ($W\cdot °C^{-1}$), C for heat capacitance of the animal ($J\cdot °C^{-1}$) assuming a specific heat of $3.45\ J\cdot g^{-1}\cdot °C^{-1}$ (Hart 1951), PMR_n for effective net peak metabolic rate of the animal (W), and t for time (s).

The first term of this equation represents exponential cooling according to the Newtonian model in the absence of metabolic heat production. The second term represents a correction term incorporating the effects of metabolic heat production, initially slowing the rate of cooling (t small) and finally establishing an equilibrium body temperature (t large) equivalent to the ratio of PMR_n/h_{na}.

Statistics.—The separate relationships of the index of homeothermy, peak metabolic rate, and minimal thermal conductance to neonatal body mass within different families were first compared by testing the

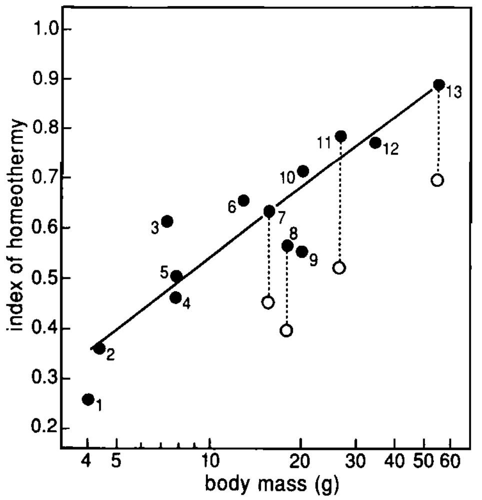

Fig. 1. Index of homeothermy as function of body mass in neonates of shorebirds (solid circles). Diagonal line refers to regression for observed values (see text). Numbers refer to species listed in Table 2. Open circles refer to simulated indices of homeothermy for four European shorebird species in absence of metabolic heat production.

homogeneity of slopes among the families by analysis of covariance (interaction term). When the interaction did not differ significantly from 0, we calculated regressions using a common slope and tested the homogeneity of intercepts (family effect). When this effect was significant, we tested the difference between the intercepts of each family using the LSMEANS/PDIFF option in the GLM procedure of SAS (SAS Institute 1988). This is an *a posteriori* test without preplanned comparisons and the statistics should be evaluated conservatively. Therefore, we used a probability level of 0.01 to determine statistical significance.

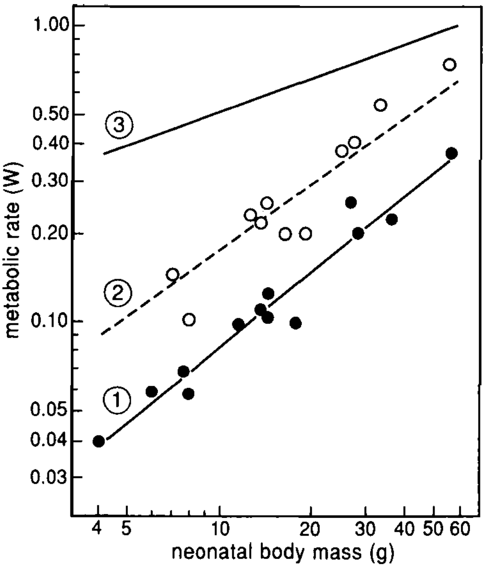

Fig. 2. Resting (solid circles) and peak (open circles) metabolic rates in neonates of shorebirds as function of body mass. Line 1 refers to relation between basal metabolic rate and body mass in neonates according to formula $BMR = 0.0114M^{0.855}$ (Klaassen and Drent 1991; data on 84 species). Line 2 refers to relationship between BMR and body mass in adult shorebirds according to formula BMR (W) $= 5.06M^{0.729}$, M in kg (Kersten and Piersma 1987). Line 3 refers to required effective net peak metabolic rate to achieve full homeothermy at 18°C.

RESULTS

Cooling rates.—Results from the experiments on cooling rates are presented in Figure 1, where index of homeothermy (H) is graphed as a function of neonatal body mass. The basic infor-

TABLE 2. Body mass, initial temperature (T_i) and index of homeothermy (H) in neonates of shorebirds.

Species	Mass (g)	T_i (°C)	H	SE[a]	n
1 Least Sandpiper	4.0	35.1	0.26	—	1
2 Red-necked Phalarope	4.3	36.0	0.36	0.13	2
3 Semipalmated Plover	7.0	35.1	0.61	0.02	3
4 Stilt Sandpiper	7.5	38.0	0.46	0.04	3
5 Dunlin	7.6	36.6	0.50	0.07	3
6 Lesser Yellowlegs	12.5	39.2	0.65	0.08	3
7 Common Redshank	15.1	39.7	0.63	0.03	6
8 Northern Lapwing	17.6	38.2	0.57	0.02	16
9 Hudsonian Godwit	19.2	39.0	0.55	—	1
10 Lesser Golden-Plover	19.7	38.3	0.71	0.01	2
11 Black-tailed Godwit	26.0	39.6	0.78	0.02	13
12 Whimbrel	33.5	37.0	0.77	0.06	3
13 Eurasian Curlew	53.9	39.2	0.88	0.02	7

[a] SE of H.

TABLE 3. Body mass (*M*; g), resting metabolic rate (*RMR*; W), peak metabolic rate (*PMR*; W), and minimal thermal conductance (*h*; $\mathrm{mW \cdot g^{-1} \cdot {}^{\circ}C^{-1}}$) in neonates of shorebirds.[a]

Species	*M*	*RMR*	SE	*n*	*M*	*PMR*	SE	*n*	*M*	*h*	SE	*n*
1	4.0	0.040	—	—	—	—	—	—	—	—	—	1
3	6.0	0.059	—	1	7.0	0.147	—	1	7.0	3.57	—	1
4	7.9	0.058	—	1	—	—	—	—	—	—	—	—
5	7.6	0.069	0.018	3	7.9	0.102	—	1	7.9	3.95	—	1
6	11.5	0.098	—	1	12.5	0.229	—	—	—	—	—	—
14	13.6	0.110	0.004	5	13.6	0.217	0.021	3	14.1	1.95	0.13	6
7	14.2	0.106	0.004	5	14.3	0.251	0.007	6	14.4	1.75	0.05	9
8	17.1	0.106	0.006	7	16.2	0.199	0.021	5	16.7	2.10	0.05	10
10	14.2	0.126	—	1	19.0	0.200	—	1	19.0	2.51	—	1
9	26.2	0.255	—	1	24.6	0.382	—	1	25.9	1.87	—	1
11	27.8	0.202	0.026	7	27.0	0.403	0.017	6	27.7	1.47	0.07	9
12	35.2	0.223	—	1	32.5	0.517	0.034	3	32.5	1.84	0.43	3
13	55.6	0.368	0.014	10	54.1	0.726	0.031	6	56.3	0.82	0.03	10

[a] Species numbers as listed in Table 2, with addition of 14 for the Ruff. *M*, body mass (g). *RMR*, resting metabolic rate in thermoneutral zone (W). *PMR*, peak metabolic rate (W). *h*, minimal thermal conductance ($\mathrm{mW \cdot g^{-1} \cdot {}^{\circ}C^{-1}}$).

mation is presented in Table 2. The relation between the index of homeothermy and neonatal body mass in shorebirds can be described by

$$H = 0.073 + 0.464 \log_{10}(M) \qquad (6)$$

($F_{1,11} = 56$, $P < 0.0001$, $r^2 = 0.84$, standard error of slope [s_b] = 0.062). By extrapolation a hypothetical shorebird neonate of about 100 g would be fully homeothermic ($H = 1$) at 18°C, over 30 min. For the four European species we also graphed the simulated indices of homeothermy (open circles) in the absence of metabolic heat production (see below).

Metabolic rates and minimal thermal conductances.—In Figure 2 the values for resting metabolic rates in the zone of thermoneutrality (*RMR*; solid circles) are graphed against the neonatal body mass. The regressions relating basal metabolic rate to body mass in neonates of different families (Klaassen and Drent 1991) and in adult shorebirds (Kersten and Piersma 1987) are drawn for comparison. The basic information is presented in Table 3. The regression for resting metabolic rate as a function of neonatal body mass in shorebirds can be described by

$$RMR\ (\mathrm{W}) = 0.0118M^{0.855} \qquad (7)$$

($F_{1,11} = 16$, $P < 0.0001$, $r^2 = 0.96$, $s_b = 0.052$). The slope of the regression for neonates did not differ statistically ($P = 0.14$) from the slope for adult shorebirds (0.729; Kersten and Piersma 1987). Assuming a common slope of 0.802 ($F_{1,16} = 382$, $P < 0.0001$, $s_b = 0.041$), the resting metabolic rate in shorebird neonates is about 60% of the adult level (intercept of log-transformed values for adults = −1.638, $s_b = 0.090$; difference between neonate and adult intercept = −0.230 ± 0.049, $F_{1,16} = 22$, $P = 0.0002$; total $R^2 = 0.99$).

In Figure 2 the peak metabolic rates (*PMR*; open circles) are graphed against neonatal body mass. The regression for peak metabolic rate as a function of neonatal body mass can be described by

$$PMR\ (\mathrm{W}) = 0.0205M^{0.892} \qquad (8)$$

($F_{1,9} = 76$, $P < 0.0001$, $r^2 = 0.89$, $s_b = 0.102$). Using analysis of covariance, we determined that the slopes for peak and resting metabolic rates in the thermoneutral zone did not differ ($P = 0.74$). Furthermore, the two regressions had a common slope of 0.868 ($F_{1,21} = 300$, $P < 0.0001$, $s_b = 0.050$), and the intercepts of the log-transformed values (−1.94 for thermoneutral zone, and −1.66 for peak metabolic rate) differed by a factor of 1.91 ($F_{1,21} = 97$, $P < 0.0001$, total $R^2 = 0.96$). In Figure 2, we also graphed the peak metabolic rate that is required for a shorebird neonate to maintain its body temperature at 38°C, at an ambient temperature of 18°C (indicated by 3; see Discussion).

In Figure 3 the values for the minimal thermal conductance (*h*) are graphed against the neonatal body mass. The regression for adult nonpasserine birds measured during daytime (Aschoff 1981) is drawn for comparison. The regression for minimal thermal conductance as a function of neonatal body mass in shorebirds can be described by

$$h\ (\mathrm{mW \cdot {}^{\circ}C^{-1} \cdot g^{-1}}) = 12.485M^{-0.629} \qquad (9)$$

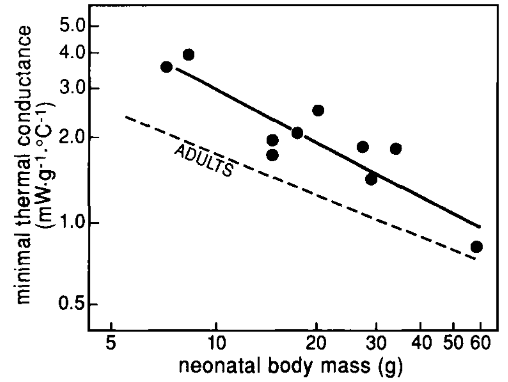

Fig. 3. Minimal thermal conductance in neonates of shorebirds as function of body mass. Solid line refers to regression for shorebird neonates. Broken line refers to minimal thermal conductance in adult nonpasserine birds at daytime ($h = 5.25M^{-0.484}$; Aschoff 1981).

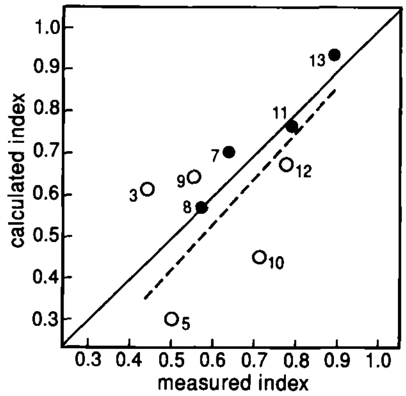

Fig. 4. Calculated indices of homeothermy derived from Newtonian cooling model with data on effective peak metabolic rate and dry thermal conductance obtained from metabolic measurements, in relation to measured indices of homeothermy, by means of cooling experiments. Solid circles refer to European species and open circles to North American species. Numbers refer to species listed in Table 1. Drawn line refers to equality between calculated and observed indices. Broken line refers to fitted relationship between calculated and measured indices of homeothermy.

($F_{1,8} = 33.8$, $P < 0.001$, $r^2 = 0.81$, $s_b = 0.108$). Using analysis of covariance we determined that the slope for neonates did not differ significantly from the slope of -0.484 for adult nonpasserine birds during daytime (Aschoff 1981; $P = 0.40$). Furthermore, the two regressions had a common slope of -0.518 ($F_{1,46} = 936$, $P < 0.0001$, $s_b = 0.017$) and the intercepts of the log-transformed data (0.958 for shorebird neonates, and 0.756 for adults) differed by a factor of 1.59 ($F_{1,46} = 26.3$, $P < 0.0001$, total $R^2 = 0.96$).

Simulation of cooling curves with Newtonian cooling model.—We can use the Newtonian cooling model to simulate cooling curves for each species by using the species-specific values for the peak metabolic rate and minimal thermal conductance, derived from the metabolic measurements corrected for the evaporative heat loss (Bakken 1976, see Materials and Methods). For the simulation, the initial body temperature for each species was taken from Table 2, and the ambient temperature as 18°C. Figure 4 gives the relation between the observed index of homeothermy, as determined from the cooling trials, and the simulated values, as determined from the metabolic data and the Newtonian cooling model. As a reference we drew the line for equality of observed and simulated values. From the data we calculated the following regression:

$$H(\text{simulated}) = -0.148 + 1.13H(\text{observed}), \tag{10}$$

($F_{1,7} = 8.86$, $P < 0.05$, $r^2 = 0.50$). The standard error of the slope and the Y-intercept were 0.380, and 0.258, respectively. Thus, the slope and the intercept of the regression do not statistically differ from 1 and 0, respectively. The calculated index of homeothermy for the European species was on average within 5% of observed values. The low agreement of calculated and observed indices in some North American species, may have reflected the limited data available to estimate H and metabolic rates. Therefore, the Newtonian cooling model, with the values derived from metabolic measurements, appears to give a consistent description of the rate of body cooling.

In order to demonstrate the influence of metabolism on body cooling we compared our observations with a simulation of body cooling in the absence of heat production. We used the preceding model with only species-specific data for minimal dry thermal conductance for the four European species. The initial body temperatures were taken from Table 2, and the ambient temperature was 18°C. The cooling time was 30 min. The simulated indices of homeothermy are presented in Figure 1 (open circles). As can be seen, the simulated values in the absence of metabolic heat production are well below those we measured with the cooling trials.

For the four species, the simulated body temperatures after 30 min were 28.9°C on average. In contrast, the observed values were on average 33.2°C.

DISCUSSION

Time budgets in the field.—In the field, shorebird chicks allocate their time between alternating bouts of foraging and parental brooding (Norton 1973, Chappell 1980, Beintema and Visser 1989a, Visser et al. 1989). Norton (1973) observed that postbrooding body temperatures of shorebird chicks were about 38°C, and that they allowed their body temperatures to drop to about 30°C before being brooded again. Norton pointed out that this tolerance of lower body temperature leads to an increase in the amount of time available for foraging at low metabolic cost of homeothermy to the chick and, consequently, to increases in both the daily food intake and allocation of assimilated energy to growth.

With the Newtonian cooling model we can investigate the importance of neonatal body mass and ambient temperature upon the cooling rate of a generalized shorebird chick. The interspecific relation between the effective net peak metabolic rate and body mass for shorebird neonates can be described by

$$PMR_n\ (\mathrm{W}) = 0.0161M^{0.922} \qquad (11)$$

($F_{1,9} = 58.0, P < 0.001, r^2 = 0.85, s_b = 0.121$), and between the minimal dry thermal conductance per individual and body mass by

$$h_{na}\ (\mathrm{W \cdot {}^{\circ}C^{-1}}) = 0.0114M^{0.359} \qquad (12)$$

($F_{1,8} = 9.22, P < 0.016, r^2 = 0.48, s_b = 0.118$).

To investigate the implications for neonatal time budgets of a reduced tolerance to lower body temperatures, we applied these formulae in the Newtonian cooling model to estimate the period required for a chick to cool from 38 to 30°C, and from 38 to 34°C, as a function of body mass at ambient temperatures of 5 and 15°C. The body temperature range between 38 and 30°C is probably experienced by shorebird chicks of different ages under field conditions (see above). The results of the simulations are graphed in Figure 5. The graph clearly shows the importance of neonatal body mass and ambient temperature. As can be seen from the cooling times at an ambient temperature of 15°C, a shift in tolerance to lower body temperatures will prolong the duration of cooling; this effect increases with body mass. At ambient temperatures slightly higher than 15°C, large neonates will not cool below 30°C, further emphasizing the significance of a tolerance of lower body temperature. We do not know the extent to which brooding time will be affected by body temperature at the onset of brooding. During brooding, most heat is transferred directly from the brood patch of the parent to the chick. This heat flow will be increased by a higher temperature gradient between parent and chick. Chappell (1980), using internally heated Wood's alloy casts covered with natural integument, determined heating and cooling times of chicks of several shorebird species under natural or simulated natural conditions. The time required to heat from 30 to 38°C under simulated brooding at an ambient temperature of 0°C (about 6 min) was independent of body mass between 5 and 21 g. Cooling time varied from 4 min for 5-g chicks to 15 min for 20-g chicks. Chappell concluded, on the basis of additional calculations, that extending the range of body temperature tolerance would result in increased foraging time per day.

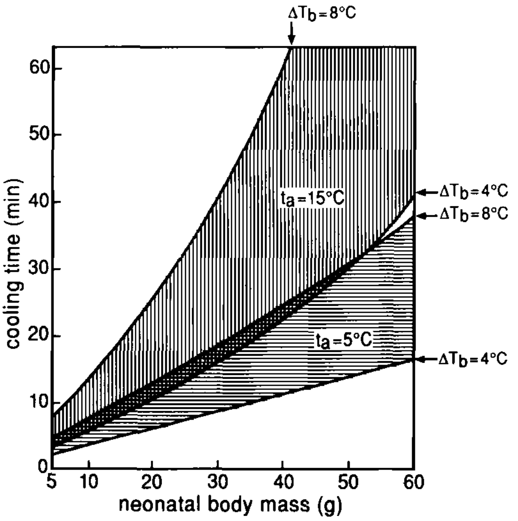

Fig. 5. Estimated time periods for neonates to cool from 38 to 30°C ($\Delta T_b = 8$), or to cool from 38 to 34°C ($\Delta T_b = 4$) at ambient temperatures of 5 (horizontal hatching) and 15°C (vertically hatched) as function of body mass. Estimates derived from Newtonian cooling model.

Field observations on neonates of the Common Redshank, Northern Lapwing and Black-tailed Godwit revealed foraging periods at ambient temperatures of 15°C of 6.5, 8.1 and 7.4

min, respectively (Beintema and Visser 1989a). These were much shorter than predicted from the Newtonian cooling model for a decrease in body temperature from 38 to 30°C. This may suggest that neonates cooled faster at lower ambient temperatures when foraging in the field (possibly due to disturbance of the boundary layer, when walking, which leads to an increase in thermal conductance), or that neonates did not always allow their body temperatures to drop to 30°C. The chicks in the field may have experienced the effect of wind, to which the thermal conductance of the downy plumage is very sensitive (Chappell 1980). An avenue as yet unexplored is the modelling of cooling and rewarming trajectories in order to maximize feeding time given the cost constraint on the chick.

Ratio of heat production to heat loss.—As was shown in Figure 5, the cooling time, and thus the degree of homeothermy, can be considered as a function of ambient temperature and body mass. We can obtain some insight into the physiological basis of this relationship from the Newtonian cooling model

$$T_e = T_a + PMR_n/h_{na}, \tag{13}$$

in which T_e stands for the equilibrium body temperature of a cooling experiment. According to this equation, T_e is a function of ambient temperature and the ratio of heat production to heat loss (PMR_n/h_{na}; °C). This ratio is equal to the temperature difference above the ambient temperature that can be maintained by the chick. By applying the aforementioned interspecific regressions relating effective net peak metabolic rate and minimal dry thermal conductance to body mass in shorebird neonates, we can investigate the importance of neonatal body mass upon the ratio PMR_n/h_{na}. This ratio can be described by

$$PMR_n/h_{na} = 0.0161M^{0.922}/0.0114M^{0.359}, \tag{14}$$

or by

$$PMR_n/h_{na} = 1.412M^{0.563}. \tag{15}$$

Therefore, the main conclusion is that larger neonates have a more favorable ratio between heat production and heat loss and, consequently, a higher degree of homeothermy compared to smaller neonates.

Heat production required to achieve homeothermy.—It is of interest to determine how much heat a small chick would have to produce to maintain its body temperature. We used the Newtonian cooling model to calculate the effective net peak metabolic rate required to maintain the body temperature of the chick at 38°C (which is the average initial body temperature, Table 2), at an ambient temperature of 18°C (ambient temperature at which indices of homeothermy were determined) as a function of body mass. The relationship can be described by

$$PMR_n = 0.228M^{0.359}, \tag{16}$$

and is drawn in Figure 2 (curve 3). The equation shows that small neonates would have to elevate their metabolic rate to a factor of about 10 times the resting metabolic rate, and large neonates to a factor of about 3. This would increase the amount of time available for foraging, but at high cost, perhaps much more than the potential increase in food intake. To support such a high energy expenditure, the chick would probably require a digestive system with a greatly enhanced capacity. According to Kirkwood (1983) maximum metabolizable energy in birds and mammals does not exceed four to five times the basal metabolic rate. In addition, a high thermogenic capacity would require a highly specialized function of the skeletal muscle. Such a high maturity of muscle function may limit the growth rate of the tissue and prolong postnatal development (Ricklefs 1979). From an energetic point of view, for a chick it is important to maximize the rate of food intake with a minimum of cost thereby increasing the efficiency of growth.

Comparison between shorebirds and other families.—We were able to find literature data on cooling rates (at an ambient temperature of 15–20°C, during about 30 min), peak metabolic rates and minimal thermal conductances of neonates in the following families (Table 4): ducks (Anatidae), grouse and pheasants (Phasianidae), and gulls and terns (Laridae).

The slopes of the regressions of the index of homeothermy (H) on the logarithm (base 10) of neonatal mass did not differ significantly among families ($P = 0.37$). The common slope was 0.452 ($F_{1,21} = 104$, $P < 0.0001$, $s_b = 0.044$). The intercepts indicated that the Anatidae had significantly higher values of H than the other families, and that the Phasianidae had higher values than the Scolopacidae/Charadriidae and Laridae (Table 5).

For the peak metabolic rates, slopes of log-

TABLE 4. Body mass, index of homeothermy, peak metabolic rate, and minimal thermal conductance in neonates of Anatidae, Phasianidae, and Laridae.[a]

Species	M	H	PMR	h	Source
		Anatidae			
Anas crecca	16.8	0.97	>0.75	1.65	1
A. penelope	26.4			1.15	1
A. platyrhynchos	28.8	0.96	>0.98	1.28	1
Clangula hyemalis	28.7	1.00			2
Bucephala clangula	32.4	0.95		1.04	1
Aythya fuligula	34.1			0.99	1
A. ferina	40.1			1.00	1
Mergus serrator	44.2			0.86	1
M. merganser	46.2			0.87	1
Melanitta fusca	54.7			0.84	1
Somateria mollisima	61.4			0.59	1
Somateria mollisima	60.0		2.00		3
		Phasianidae			
Colinius virginianus	6.3		0.10	3.39	4
Coturnix c. japonica	6.5	0.52			2
Lagopus mutus	15.0	0.70			5
L. lagopus	15.1	0.76	0.23		1, 6
Phasianus colchicus	18.0	0.75			7
Lyrurus tetrix	24.0	0.88			1
Tetrao urogallus	38.0	0.84			1
Gallus gallus (broiler)	45.3		0.63	0.86	8
G. gallus (layer)	44.1		0.62	0.85	8
G. gallus (layer)	40.9	0.85			9
		Laridae			
Larus atricilla	28.4		0.47	1.12	10
L. delawarensis	34.1		0.64	0.99	11
L. occidentalis wymani	58.0		0.91	0.94	12
L. o. livens	65.4		0.89	0.84	13
Larus argentatus	66.3	0.91			14
Sterna paradisaea	13.0		0.21	1.94	15
S. paradisaea	12.0	0.51			2
S. hirundo	14.9		0.21	1.64	15

[a] M, neonatal body mass (g). H, index of homeothermy. PMR, peak metabolic rate (W). h, minimal thermal conductance ($mW \cdot g^{-1} \cdot {}^{\circ}C^{-1}$). References: (1) Koskimies and Lahti (1964); (2) Ricklefs unpubl. data; (3) Grav et al. (1988); (4) Spiers et al. (1985); (5) Pedersen and Steen (1979); (6) Aulie (1976); (7) Koskimies (1962); (8) Visser and van Kampen unpubl. manuscript; (9) Visser and Zeinstra unpubl. data; (10) Dawson et al. (1972); (11) Dawson et al. (1976); (12) Dawson and Bennett (1981); (13) Dawson and Bennett (1980); (14) Hüppop (1987); (15) Klaassen and Zwaan unpubl. data.

log (base 10) regressions for each family did not differ significantly ($P = 0.79$). The common slope had a value of 0.916 ($F_{1,19} = 332$, $P < 0.0001$, $s_b = 0.050$). This slope for neonates differed significantly from the interspecific slope of 0.729 for the relationship between basal metabolic rate and body mass in adult nonpasserine birds during daytime (Aschoff and Pohl 1970). Because peak metabolic rate increases faster than surface area with increasing neonatal mass,

TABLE 5. Coefficients of equations for index of homeothermy (H), peak metabolic rate (PMR) and minimal thermal conductance (h) as a function of body mass for representatives of given avian families.

		Intercept (value at 1 g)			
Factor	Slope (SE)	Anatidae	Phasianidae	Laridae	Scolopacidae/ Charadriidae
H	0.452 (0.044)	0.332^{c}	0.117^{b}	0.055^{ab}	0.087^{a}
PMR	0.916 (0.050)	0.0494^{b}	0.0209^{a}	0.0190^{a}	0.0191^{a}
h	−0.621 (0.047)	9.221^{a}	9.550^{a}	9.780^{a}	12.274^{b}

[a,b,c] Values for families (expressed as antilogarithms of the intercepts of the log-log regressions) with the same superscripts do not differ ($P > 0.01$).

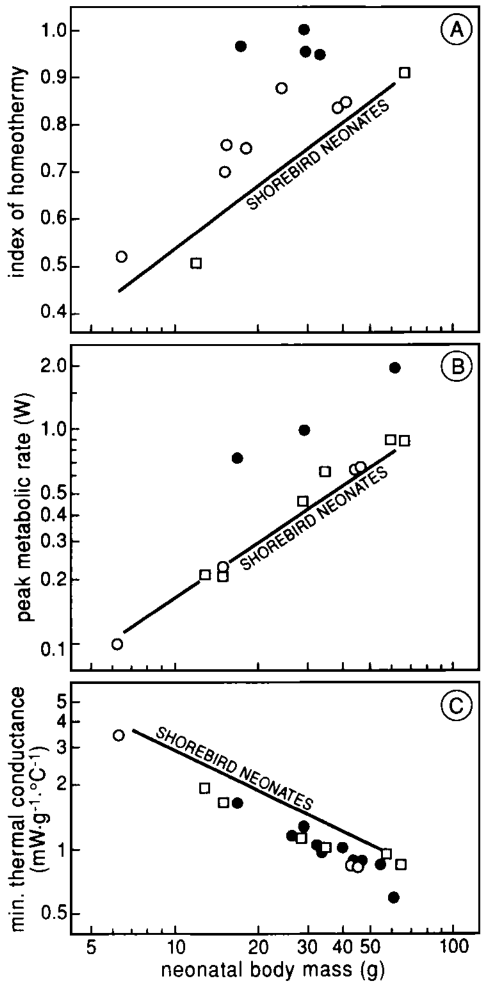

Fig. 6. Index of (A) homeothermy, (B) peak metabolic rate, and (C) minimal thermal conductance in neonates of Anatidae (solid circles), Phasianidae (open circles), and Laridae (open squares) in relation to body mass. Diagonal lines refer to interspecific allometric regressions for shorebird neonates (see Results).

larger neonates have a higher developed thermogenic capacity compared to the neonates of smaller species. The intercepts indicated that the Anatidae had significantly higher peak metabolic rates than the other families by a factor of 2.5, and that the peak metabolic rates for other families did not differ significantly (Table 5).

For the minimal thermal conductance, slopes of log-log (base 10) regressions with respect to body mass did not differ significantly among families ($P = 0.38$). The common slope had a value of -0.621 ($F_{1,24} = 178$, $P < 0.0001$, $s_b = 0.047$). The intercepts indicated that the minimal thermal conductances for Scolopacidae/Charadriidae were 20% greater than those of the Anatidae, Phasianidae and Laridae (Table 5). Possibly the higher thermal conductance of shorebirds reflects their relatively long legs and necks, and may therefore be a consequence of their body form rather than a thermal strategy. A consequence of this higher thermal conductance is that a shorebird neonate of a given body mass needs to generate more heat to maintain its body temperature than neonates of other bird families.

We compared the data for minimal thermal conductances for neonates of all families with the data on adult nonpasserine birds during daytime (Aschoff 1981). Analysis of covariance revealed that the slope of the allometric regression for minimal thermal conductance against body mass for neonates differed from the slope for adults ($F_{1,64} = 7.61$, $P < 0.01$). This relationship for neonates of all families can be described by

$$h = 13.47M^{-0.702}, \qquad (17)$$

($F_{1,27} = 182$, $P < 0.0001$, $r^2 = 0.87$, $s_b = 0.052$). A typical adult nonpasserine bird of 10 g has a minimal thermal conductance of 1.73 $\text{mW}\cdot{}^\circ\text{C}^{-1}\cdot\text{g}^{-1}$ during daytime (as predicted from the equation of Aschoff 1981) and a precocial or semiprecocial neonate of the same body mass of 2.68 $\text{mW}\cdot{}^\circ\text{C}^{-1}\cdot\text{g}^{-1}$ (i.e. 155% of adult value). For an adult and neonate of 50 g, these values are 0.79 and 0.86 $\text{mW}\cdot{}^\circ\text{C}^{-1}\cdot\text{g}^{-1}$ (i.e. 109% of adult value), respectively. Thus, in small neonates the effectiveness of the downy plumage is much lower than in large neonates. This is probably the result of the disproportionately large outer surface area of the down in small neonates, leading to a higher heat flux through the plumage (Turner 1988).

Even the smallest duck species examined appeared to be almost homeothermic at 20°C (see Fig. 6A), most species even at 10°C (Koskimies and Lahti 1964). Koskimies and Lahti reasoned that this extreme cold hardiness is an adaptation to aquatic life. However, some aquatic species breeding in the same regions, such as the Common Gallinule (*Gallinula chloropus*) and some grebes (*Podiceps cristatus* and *P. auritus*) exhibit a low degree of homeothermy at hatching (Siegfried and Frost 1975, Kespaik et al. 1968). However, young grebe chicks are not strictly aquatic in that they are often brooded on the back of the swimming parents. The high degree of homeothermy in the Anatidae is mainly a result of high peak metabolic rates (Fig. 6B). The aquatic lifestyle of ducklings seems not to involve integuments with lower thermal conductances when exposed to air, especially when compared to Phasianidae and Laridae (Fig. 6C).

Values of H for phasianid neonates significantly exceed those of scolopacid and charadriid neonates. As demonstrated before, this resulted from a lower thermal conductance of phasianid neonates compared to shorebird neonates. This higher degree of homeothermy of phasianid neonates partially compensates for the smaller relative size of the egg in Phasianidae compared to other precocial species (Rahn et al. 1975). A typical shorebird of 250 g produces an egg of 33.8 g from which a 22.6 g neonate hatches, and a typical galliform bird of the same body mass produces an egg of 16.6 g from which an 11.1 g neonate hatches (Rahn et al. 1975). The estimated indices of homeothermy for these chicks are 0.70 and 0.66, respectively; a shorebird neonate with a mass of 11.1 g would be expected to have a value of H of 0.56.

The Laridae seem to have a similar relation between neonatal body mass and degree of homeothermy as the Scolopacidae/Charadriidae, although few species were examined (Fig. 6A). This was somewhat unexpected because semiprecocial species in the Laridae are fed by their parents and, thus, food provisioning does not depend on the chick's maintaining a high body temperature. However, a high degree of homeothermy frees both parents from extensive brooding, resulting in an increase in energy intake for the family unit. However, when disturbed by a predator a high degree of homeothermy of the chick allows it to shelter in the vegetation for a longer time. This may affect the chances for survival.

In conclusion, three options seem to be available for achieving a high degree of homeothermy at hatching: (1) producing a high peak metabolic rate as observed in the Anatidae; (2) having a favorable surface-to-volume ratio, as observed in large neonates; or (3) reducing thermal conductance of the body surface. In this context, the high thermal conductance of neonatal shorebirds compared to similarly sized neonates in other precocial taxa presents an enigma. The shorebirds are more similar in thermoregulation to semiprecocial species in the Charadriiformes (Laridae) than they are to the species in the Anatidae in that young chicks rely more upon parental sources of heat than their own thermogenesis. Members of Galliformes appear to be intermediate. Apparently, these patterns reflect the most efficient use of energy and time for the family unit, given brood size, habitat, and dispersion of the family group.

Degree of homeothermy and geographical distribution.—Koskimies and Lahti (1964) demonstrated a relationship between the degree of homeothermy in ducklings and their geographical distribution. No such relationship appears to exist in the shorebird species we studied. The Red-necked Phalarope and Least Sandpiper, with neonates having poor thermoregulation, breed even slightly further north (up to about 75°N; Johnsgard 1981) than the Eurasian Curlew (up to 72°N), of which the neonates are excellent thermoregulators. Also the Northern Lapwing, which has a relatively poor degree of homeothermy with respect to body mass, breeds up to 71°N. Dawson and Bennett (1980) similarly failed to find a relation between the degree of homeothermy in neonates of gulls and the species' geographical distribution.

Large body size conveys an advantage to chicks with respect to maintenance of body temperature. Among precocial species, the neonates of shorebirds and gulls are relatively large (Rahn et al. 1975), which may provide them increased thermal inertia. However, there appears to be no general relationship between body size in shorebirds and latitude, the smallest species being some of the most northerly distributed of the group. The eggs and neonates of these species are not large compared to relatives breeding at lower latitudes. Thus, these species must employ mechanisms other than large body mass to enable them to breed in cold environments.

The terrestrial chicks of shorebirds and gulls can, even at high latitudes, benefit from favorable microhabitats, especially under sunny conditions (Klaassen et al. 1989) and with parental brooding. Aquatic ducklings (especially the sea ducks) are less able to select warm microhabitats and, therefore, have to rely more on their heat production to maintain their body temperature.

The cooling time (or potential foraging time) of the chick is determined by the heat production and thermal conductance of the integument of the neonate, in combination with the ambient temperature. Availability of prey determines whether this amount of time is sufficient for the chick to obtain a positive energy balance. In Dutch agricultural grasslands young chicks of the Northern Lapwing and Black-tailed Godwit needed to forage for about 5 h per day to maintain constant body mass (Beintema and Visser 1989a). In the tundra habitats, during the burst of emergence of chironomids and tipulids in the arctic summer, chicks may need much less time and may profit from the continuous daylight, which results in an increase in the time available for foraging per day.

We would expect species with small neonates to begin breeding somewhat later in the season so as to benefit from higher ambient temperatures. In The Netherlands, the fact that the smaller Ruff and Common Redshank begin to breed after the larger Black-tailed Godwit and Eurasian Curlew is consistent with this idea. However, the Northern Lapwing starts breeding earlier than the larger species (Beintema and Visser 1989b), although the degree of homeothermy in Northern Lapwing neonates is much lower. This suggests that factors in addition to the degree of homeothermy affect the timing of the breeding season.

The parent and young chick of precocial species are intimately tied together through the dependence of the chick upon the parent for the maintenance of body temperature. This relationship varies both during the course of development, between the different taxa, and in relation to weather conditions and availability of food. Thus, the parent-chick unit provides an excellent opportunity for studying the interrelationship of development and parental care.

ACKNOWLEDGMENTS

The investigations were supported by the Foundation for Biological Research (BION), which is subsidized by the Netherlands Organization for Scientific Research (NWO), under Grant #427.181. L. van der Bergh collected the eggs, and D. van Dijk took care of the chicks. A. Doornenbal, O. van der Beek and J. Hydra are acknowledged for their technical support. E. Zeinstra collected and processed most of the data on cooling rates. H. van Biezen gave statistical support. G. van Beek commented on heat-transfer analysis in animals, and he provided a computer program to simulate the cooling curves. M. van Kampen was helpful by designing the experimental setup, and is acknowledged for his stimulating discussions on physiological processes in birds. D. Visser drew the figures. A. Beintema, M. Dietz, R. Drent, G. Huisman, M. van Kampen and E. Zeinstra commented on earlier drafts of this paper.

Fieldwork at Churchill was supported by the Division of Polar Programs of the National Science Foundation (USA) and was carried out at the Churchill Northern Studies Centre with the assistance of Kenneth Baker, Larry Clark, and David Goldstein (NSF grants DPP7908571 and BSR 90-07000 to RER).

LITERATURE CITED

ASCHOFF, J. 1981. Thermal conductance in mammals and birds: Its dependence on body size and circadian phase. Comp. Biochem. Physiol. A Comp. Physiol. 69A:611–619.

ASCHOFF, J., AND H. POHL. 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29:1541–1552.

AULIE, A. 1976. The pectoral muscles and the development of thermoregulation in chicks of Willow Ptarmigan (*Lagopus lagopus*). Comp. Biochem. Phsyiol. A Comp. Physiol. 53A:343–346.

BAKKEN, G. S. 1976. A heat transfer analysis of animals: Unifying concepts and the application of metabolism chamber data to field ecology. J. Theor. Biol. 60:337–384.

BEINTEMA, A. J., AND G. H. VISSER. 1989a. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77:181–192.

BEINTEMA, A. J., AND G. H. VISSER. 1989b. Growth parameters in chicks of charadriiform birds. Ardea 77:169–180.

CHAPPELL, M. A. 1980. Thermal energetics of chicks of arctic-breeding shorebirds. Comp. Biochem. Physiol. A Comp. Physiol. 65A:311–317.

DAWSON, W. R., AND A. F. BENNETT. 1980. Metabolism and thermoregulation in hatchling Western Gulls (*Larus occidentalis livens*). Condor 82:103–105.

DAWSON, W. R., AND A. F. BENNETT. 1981. Field and laboratory studies of the thermal relations of hatchling Western Gulls. Physiol. Zool. 54:155–164.

DAWSON, W. R., A. F. BENNETT, AND J. W. HUDSON. 1976. Metabolism and thermoregulation in hatchling Ring-billed Gulls. Condor 78:49–60.

DAWSON, W. R., J. W. HUDSON, AND R. W. HILL. 1972. Temperature regulation in newly hatched Laughing Gulls (*Larus atricilla*). Condor 74:177–184.

GRAV, H. J., B. BORCH-IOHNSON, H. A. DAHL, G. W. GABRIELSEN, AND J. B. STEEN. 1988. Oxidative capacity of tissues contributing to thermogenesis in Eider (*Somateria mollissima*) ducklings: Changes associated with hatching. J. Comp. Physiol. B 158: 513–518.

HART, J. S. 1951. Calorimetric determination of average body temperature of small mammals and its variation with environmental conditions. Can. J. Zool. 29:224–233.

HÜPPOP, O. 1987. Der Einfluss von Wachstum, Thermoregulation und Verhalten auf den Energiehaushalt der Silbermöwe, *Larus argentatus*. Ph.D. dissertation, Univ. Hamburg, Hamburg.

JOHNSGARD, P. A. 1981. The plovers, sandpipers, and snipes of the world. Univ. Nebraska Press, Lincoln.

KERSTEN, M., AND T. PIERSMA. 1987. High levels of energy expenditure in shorebirds: Metabolic adaptations to an energetically expensive way of life. Ardea 75:175–187.

KESKPAIK, J., S. ONNO, AND A. DAVYDOV. 1968. Development of thermoregulation among nestling *Podiceps cristatus* and *Podiceps auritus* during ontogenesis. Publ. Acad. Sci. Estonian SSR, Biol. Ser. 2, 17:192–205.

KIRKWOOD, J. K. 1983. A limit to metabolizable energy intake in mammals and birds. Comp. Biochem. Physiol. A Comp. Physiol. 75A:1–3.

KLAASSEN, M., C. BECH, D. MASMAN, AND G. SLAGSVOLD. 1989. Energy partitioning in Arctic Tern chicks (*Sterna paradisaea*) and possible metabolic adaptations in high latitude chicks. Pages 339–347 *in* Physiology of cold adaptation in birds (C. Bech and R. E. Reinertsen, Eds.). Plenum Press, New York.

KLAASSEN, M., AND R. H. DRENT. 1991. An analysis of hatchling resting metabolism: In search of ecological correlates that explain deviations from allometric relations. Condor 93:612–629.

KOSKIMIES, J. 1962. Ontogeny of thermoregulation and energy metabolism in some gallinaceous birds. Pages 149–160 *in* Transactions 5th Congress International Union of Game Biologists, Bologna.

KOSKIMIES, J., AND L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. Auk 81:281–307.

MCNAB, B. K. 1980. On estimating thermal conductance in endotherms. Physiol. Zool. 53:145–156.

NICE, M. M. 1962. Development of behavior in precocial birds. Trans. Linn. Soc. N.Y. 8:1–211.

NORTON, D. W. 1973. Ecological energetics of calidrine sandpipers breeding in northern Alaska. Ph.D. dissertation, Univ. Alaska, Fairbanks.

PEDERSEN, H. C., AND J. B. STEEN. 1979. Behavioural thermoregulation in Willow Ptarmigan chicks *Lagopus lagopus*. Ornis Scand. 10:17–21.

RAHN, N., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian egg weight to body weight. Auk 92: 750–765.

RICKLEFS, R. E. 1979. Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. 54:269–290.

RICKLEFS, R. E. 1987. Characterizing the development of homeothermy by rate of body cooling. Funct. Ecol. 1:151–157.

RICKLEFS, R. E., AND D. D. ROBY. 1983. Development of homeothermy in the diving petrels *Pelecanoides urinatrix exsul* and *P. georgicus*, and the Antarctic Prion *Pachyptila desolata*. Comp. Biochem. Physiol. A Comp. Physiol. 75A:307–311.

ROMIJN, C., AND W. LOKHORST. 1961. Some aspects of energy metabolism in birds. Pages 49–58 *in* Proceedings Second Symposium on Energy Metabolism, Wageningen.

SAS INSTITUTE. 1988. SAS user's guide: Statistics, version 5 ed. SAS Institute, Inc., Cary, North Carolina.

SCHMIDT-NIELSEN, K. 1975. Animal physiology. Cambridge Univ. Press, London.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. 99:237–258.

SIEGFRIED, W. R., AND P. H. G. FROST. 1975. Continuous breeding and associated behaviour in the Moorhen, *Gallinula chloropus*. Ibis 117:102–109.

SPIERS, D. E., T. ADAMS, AND R. K. RINGER. 1985. Homeothermic development in the Bobwhite (*Colinius virginianus*). Comp. Biochem. Physiol. A Comp. Physiol. 81A:921–927.

TURNER, J. S. 1988. Body size and thermal energetics: How should thermal conductance scale? J. Therm. Biol. 13:103–117.

VISSER, G. H. 1991. Development of metabolism and temperature regulation in precocial birds. Ph.D. dissertation, Univ. Utrecht, Utrecht, The Netherlands.

VISSER, G. H., A. J. BEINTEMA, AND M. V. KAMPEN. 1989. Development of thermoregulation in chicks of charadriiform birds. Pages 725–730 *in* Thermal physiology 1989 (J. B. Mercer, Ed.). Elsevier, Amsterdam.